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Leaf litter decomposition in Guinean savannah streams

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ABSTRACT

Low-order streams of Upper Guinea receive substantial leaf litter inputs and are characterized by intermittent flow. The ecosystem functioning of such streams flowing in savannah, a common tropical vegetation and the dominant biome in West Africa, remains largely overlooked. We hypothesized litter decomposition in such streams to be (1) fast due to the expectedly high nutrient content of tropical litter, and (2) mostly driven by microorganisms due to the widely revealed paucity of tropical macroinvertebrate consumers, and even exacerbated in these systems by water temporariness. Decomposition rates of 2 common riparian tree species, *Alchornea cordifolia* and *Pterocarpus santalinoides*, in 2 streams ranged from 0.0287 to 0.0649 d⁻¹. The process was clearly governed by microbial decomposers, as shown by the exceptionally low mass loss discrepancy between fine and coarse mesh bags, a lack of shredders, and high leaf-associated fungal biomass (measured as ergosterol: up to 0.92 and 0.37 mg g⁻¹ litter of ash-free dry mass for *Alchornea* and *Pterocarpus*, respectively), together with moderate conidial production rate. In such savannah streams, the absence of leaf-shredding invertebrates seems to be compensated by a high microbial activity, providing an ultimate case for the reported preponderance of microbial decomposers over invertebrate decomposers at low latitudes. In contrast with temperate temporary streams, the processing of leaf litter from riparian trees, characterized by high nitrogen and phosphorus content, is sufficiently fast to be unaffected by flow intermittency.

Introduction

Leaf litter decomposition is known as a crucial process for stream ecosystems worldwide (Wallace et al. 1997, Gessner et al. 2010). A large proportion of streams, especially low-order forested streams, receive considerable amounts of organic matter in the form of plant litter (mainly leaves) from riparian or surrounding trees, which is metabolized as a source of carbon and nutrients and incorporated into the detrital food web by decomposer activity (Benfield 1997, Graça 2001, Gessner et al. 2007). Although well documented from temperate regions (Abelho 2001), the importance of litter input and subsequent decomposition also holds at low latitudes, yet this process has received much less attention in tropical streams. Most studies have dealt with either or both of the intrinsic and extrinsic biotic drivers of litter decomposition, specifically litter quality and decomposer activity, respectively. From one aspect, the examination of litter quality has led to diverging conclusions. Litter quality was reported to be lower in the tropics than at higher latitudes (Makkonen et al. 2012, García-Palacios et al. 2016), but Yuan and Chen (2009) found a consistently higher nitrogen (N) content and

lower phosphorus (P) content in senesced leaves from tropical forests compared to other biomes, suggesting that P may limit decomposer activity. From another aspect, according to Irons et al. (1994) the relative contribution of the 2 main leaf litter decomposers, leaf-shredding macroinvertebrates (shredders) and fungi, would tend to shift along the latitudinal gradient, dominating in temperate and tropical regions, respectively. This possibility is well supported by data from global-scale experiments (Boyero et al. 2011b, 2012), but the conclusions are generally drawn from a limited number of tropical streams that furthermore exhibit a broad across-site variability in both litter decomposition rates (Boyero et al. 2015) and relative importance of leaf-shredding macroinvertebrates (Boyero et al. 2009).

Little information on leaf litter decomposition is available from West Africa. A recent study from streams running at low/mid-altitude in Forested Guinea reported high decomposition rates, possibly due to exceptionally high N content in leaves and the dominance of fungi over leaf-shredding macroinvertebrates (Tenkiano and Chauvet 2017). Large-bodied, potentially efficient shredders (freshwater shrimps) occurred in these streams, but

their notably low density resulted in a marginal effect on leaf fragmentation, as illustrated by one-order magnitude discrepancies in microbial- and invertebrate-driven decomposition rates. In contrast with southern streams of Forested Guinea, a number of streams and rivers of Upper Guinea flow in savannah, a common tropical vegetation and the dominant biome in West Africa. In Upper Guinea, savannah is typically composed of tall grasses and shrubs associated with sparse trees, which become denser along streams and rivers. In this region, rainfall is condensed into 5 months of the year, and most rivers (especially smaller) suffer a long period of drought. As a consequence, some stream sections may dry out while others persist as temporary pools fed by groundwater seepage. Benthic communities can thus maintain until flow resumes, generally from June. Because these streams of Upper Guinea receive substantial inputs of leaf litter, even in cultivated areas, their fate and use by decomposers are questionable given the specificity of flow regime and possible implications for the decomposer communities.

Data on leaf litter decomposition and involved organisms from streams in savannah are invaluable when considering the wide extent of this biome. The only region of tropical savannah where this ecosystem process has received some attention is the Cerrado in central Brazil (Gonçalves et al. 2006, Wantzen and Wagner 2006). In Cerrado streams, leaf decomposition is slowed by the rarity of shredders and the exceptionally low levels of dissolved nutrients in water (Gonçalves et al. 2007, Morretti et al. 2007). Nevertheless, even from this region information remains scarce, and findings cannot be extended to other savannah streams because of Cerrado peculiarities. The lack of knowledge about savannah streams is particularly detrimental, not only because of their representativeness in the tropics, especially in Africa, but also when generalization about organic carbon cycling across broad latitudinal patterns is required (Boyero et al. 2011b). Documenting litter decomposition in savannah streams is also relevant in the context of the growing global warming concern because West Africa is a region expected to endure severe warming during the early and late 21st century (IPCC 2013), which may have serious consequences, depending on process modalities including decomposers' relative contribution.

To address these issues, we examined the decomposition of 2 common leaf litter species in 2 streams of Upper Guinea exhibiting a flow regime typical of savannah. Our *a priori* hypotheses were that litter decomposition in such streams would be (1) fast because of the expectedly high litter nutrient content, in line with previous results from Forested Guinea, and (2) mostly driven by microorganisms because of the widely reported

paucity of tropical macroinvertebrate consumers, exacerbated in these systems by water temporariness.

Study sites

This study was conducted in 2 streams near the city of Kankan in Upper Guinea (Western Africa). Boutroun (10°41'45.8"N, 9°28'57.5"W; 378 m a.s.l.) and Djodon (10°30'13.1"N, 9°28'16.2"W; 374 m a.s.l.) are second-order tributaries of the Milo River, a major tributary of the Niger River. Substratum consisted of sand, gravel, and cobbles, with silt and clay in some places. The mean stream width was 2.5 and 5 m and the mean depth 0.22 and 0.35 m, as determined on the first day of the litter decomposition experiment in Boutroun and Djodon, respectively. Some sections along stream courses endured droughts, which were generally more severe in Boutroun. Water flow at the experimental site was continuous from late June to December (Boutroun) or February (Djodon). These streams were affected by moderate anthropic activities including agriculture, clothes washing, and brick making, which did not modify their oligotrophic status (discussed later). Both streams run through a savannah landscape and are surrounded by deciduous trees of various species (e.g., *Detarium senegalensis* J.F.Gmel., *Ficus capensis* Thunb., *Macaranga heterophylla* (Müll.Arg.) Müll.Arg., *Mimosa pigra* L. 1755, *Parinari congensis* Ddr., *Uapaca heudelotii* Baill., and *Vitex doniana* Sweet). *Alchornea cordifolia* (Schumach. & Thonn.) Müll.Arg. (Euphorbiaceae) and *Pterocarpus santalinoides* L'Hér. ex DC. (Fabaceae), 2 common tree species in Western Africa and among the most abundant species in the vicinity of both streams, were selected for the litter decomposition experiment.

Methods

Experimental set-up

On 14 July 2015, we enclosed 5 g (± 0.05 g) of freshly fallen leaves from each species in 15 × 15 cm fine (FM, 0.5 mm) or coarse (CM, 9 mm) mesh bags, exposed in 3 reaches along each stream with a reach being considered as a statistical block. FM bags restricted leaf decomposition to microorganisms, whereas CM bags offered potential access to both macroinvertebrate and microbial decomposers. We deployed 48 leaf bags (i.e., 2 leaf species × 2 mesh sizes × 3 blocks × 4 sampling dates) in each stream, removing one leaf bag per leaf species, mesh size, and block from each stream after 14, 28, 42, and 59 d. In the laboratory, the decomposed leaves were individually rinsed with water to remove fine particulate matter and collect rare

macroinvertebrates (CM bags), which we stored in ethanol (70% vol/vol). Ten leaf disks (diameter: 12 mm) per sample from FM bags were cut from different leaves, avoiding the central vein, and used to determine the mycelial biomass and fungal sporulation rate (discussed later). The remaining leaf material was oven dried to constant mass (105 °C, 48 h) and weighed to the nearest 0.1 mg before grinding with a Culatti micro-hammer mill (2 mm mesh). Aliquots (~250 mg) of ground leaves were ignited in a muffle furnace (550 °C, 3 h) to determine ash content and calculate the proportion of ash-free dry mass (AFDM) in leaf dry mass. We used 5 unexposed batches of each leaf species to determine the initial AFDM and oven-dried (105 °C) mass to ambient-temperature mass ratio of leaves according to the same procedure described earlier.

Physical and chemical characteristics of streams

Water temperature was recorded by data loggers (HOBO UA-001-64, Bourne, MA, USA) every 30 min over the leaf decomposition experiment. Chemical properties were determined *in situ* with a multiparameter probe (Multi-1971, WTW, Weilheim, Germany) for conductivity, pH, and oxygen concentration, and a portable spectrophotometer (AL800, Aqualytic, Dortmund, Germany) with appropriate reagents for nitrate and P. Because of logistical constraints, these values were determined on only one occasion, coinciding with sampling on day 14 (conductivity, pH, oxygen concentration) or day 42 of litter decomposition (nutrient concentrations).

Community structure, abundance, and activity of fungal decomposers

Leaf content of ergosterol as a surrogate for mycelial biomass was determined as described in Gessner (2005a). Five of the 10 leaf disks per sample were stored in methanol/KOH in a cool place. Ergosterol extraction and saponification were achieved by heating the disks in methanol/KOH to 80 °C for 30 min before being cooled to 4 °C for 30 min. The extracts were purified using solid-phase extraction cartridges (Oasis HLB, 60 mg, 3 cc, Waters, Milford, MA, USA), and ergosterol was quantified by high-performance liquid chromatography (HPLC 360/442, Kontron, Eching, Germany). The HPLC system was equipped with a LiChroCART 250-4 LiChrospher 100 RP-18 (5 µm) column (Merck, Darmstadt, Germany) maintained at 33 °C, the mobile phase was 100% methanol with a flow rate of 1.4 mL min⁻¹, and the detector wavelength was set at 282 nm.

The other sets of 5 leaf disks were incubated at ambient temperature (26 ± 1 °C) for 48 h in Petri dishes containing 20 mL of filtered (GF/C, 1.2 µm pore size,

Whatman, Maidstone, UK) water of the corresponding stream and placed on an orbital shaker (100 rpm) to induce sporulation. Spore suspensions together with rinsing water were adjusted to 40 mL and fixed with 5 mL of 37.5% formaldehyde. From these suspensions, 10 mL aliquots were later filtered (Millipore SMWP, 5 µm pore size, Billerica, MA, USA) and stained with 0.1% (mass/vol) Trypan blue in 60% lactic acid (Gessner et al. 2003). The released spores of aquatic hyphomycete were counted under the microscope at 200× and identified using keys (e.g., Chauvet 1990, Gulis et al. 2005) and relevant literature.

Chemical composition of litter

Leaf litter contents in organic carbon and nitrogen were determined on 5 aliquots from FM bags by using an organic elemental analyzer (Flash 200, ThermoFisher Scientific, Waltham, MA, USA). The initial leaf content of total P was determined spectrophotometrically (Uvi Light XT5, Secomam, Alès, France) on an acidified solution of leaf ashes using the molybdate-blue method. The initial leaf content of cellulose and lignin was determined on 5 aliquots according to the procedure described in Gessner (2005b). Magnesium (Mg) and calcium (Ca) were determined from 5 aliquots of 100 mg of ground litter, weighted in polypropylene Digitubes (SCP Science France, Courtaboeuf). We added 4 mL of ultrapure HNO₃ (65–67% optima grade Sigma Aldrich) and placed the aliquots on a hotplate at 90 °C overnight. Digested solutions were diluted to 30 mL using ultrapure water (mQ system, Millipore) before determining Mg and Ca concentrations using a Thermo Electron IRIS Intrepid II ICP-OES (Thermo Scientific, Waltham, MA, USA). Blanks were negligible, and reference materials (NIST 1515 Apple Leaves and WEPAL-IPE-176 - Reed/*Phragmites communis*) were used to ensure adequate recovery and quality of the results.

Data analyses

Total decomposition rates (k_{total}) and microbial decomposition rates ($k_{\text{microbial}}$) were determined from the litter mass remaining in CM and FM bags, respectively, while invertebrate-driven decomposition rates ($k_{\text{invertebrate}}$) were determined from differences in litter mass remaining in CM and FM bags for each stream, block, leaf species, and exposure time. These rates of litter decomposition, k , were calculated according to the exponential model: $M_t = M_0 e^{-k \times t}$, where M_t and M_0 are the remaining and initial AFDM of leaves, respectively, and t the exposure time (in d), as derived from the decay model (Boulton and Boon 1991). Rates were determined by nonlinear regression analyses, and log-

transformed rates were compared by analysis of covariance (ANCOVA; Tukey HSD) using XLSTAT 2015.2.02.

Results

Water quality

Waters of Boutroun and Djodou were circumneutral (pH: 6.33 and 6.54, respectively) and exhibited low electrical conductivity (15.2 and 29.9 $\mu\text{S cm}^{-1}$, respectively). Oxygen concentration in Boutroun and Djodou was 6.83 and 7.04 mg L^{-1} , corresponding to 81% and 86% of saturation, respectively. Both dissolved nitrate and soluble reactive P concentrations were notably low (0.33 and 0.12 mg L^{-1} $\text{NO}_3\text{-N}$, and 0.003 and 0.023 mg L^{-1} $\text{PO}_4\text{-P}$ in Boutroun and Djodou, respectively). Water temperature recorded over leaf breakdown was relatively stable and similar, with mean values (26.3 and 25.5 $^\circ\text{C}$ in Boutroun and Djodou, respectively), but diel temperature oscillations were higher in Boutroun (>4 $^\circ\text{C}$) than in Djodou (1 $^\circ\text{C}$ on average).

Initial litter quality

Alchornea and particularly *Pterocarpus* exhibited high initial nutrient contents. N contents were (mean [SE]) 2.36% (0.20%) and 3.06% (0.05%), resulting in C/N ratios of 22.2 and 17.2 for *Alchornea* and *Pterocarpus*, respectively. P contents were 0.137% (0.001%) and 0.179% (0.001%) for *Alchornea* and *Pterocarpus*, respectively. The same discrepancy occurred in leaf content of Mg (0.192% [0.006%] and 0.270% [0.010%], respectively). The difference was, however, opposite for the litter content of Ca (1.500% [0.192%] and 0.401% [0.020%]) for *Alchornea* and *Pterocarpus*, respectively. Finally, initial contents in structural compounds were much

Table 1. Total, microbial, and invertebrate-driven litter breakdown rates of 2 leaf species (*Alchornea cordifolia* and *Pterocarpus santalinoides*) in 2 Guinean savannah streams, as determined from coarse-mesh bags, fine-mesh bags, and the difference in mass loss between coarse-mesh and fine-mesh bags, respectively. Average from $n=3$ per stream and leaf species (asymptotic standard error). Rates for stream \times leaf species treatments with the same letter within rows are not significantly different (Tukey HSD, $P > 0.05$). Microbial and invertebrate-driven litter breakdown rates differ significantly (Tukey HSD, $P < 0.0001$).

	Boutroun		Djodou	
	<i>Alchornea</i>	<i>Pterocarpus</i>	<i>Alchornea</i>	<i>Pterocarpus</i>
k_{total} (d^{-1})	0.0649 (0.0047) ^a	0.0291 (0.0020) ^b	0.0558 (0.0039) ^{a,b}	0.0287 (0.0029) ^b
$k_{\text{microbial}}$ (d^{-1})	0.0387 (0.0029) ^a	0.0195 (0.0017) ^a	0.0426 (0.0026) ^a	0.0226 (0.0022) ^a
$k_{\text{invertebrate}}$ (d^{-1})	0.0045 (0.0007) ^a	0.0040 (0.0007) ^{a,b}	0.0006 (0.0009) ^b	0.0019 (0.0007) ^b

higher in *Pterocarpus* (cellulose: 28.3% [1.5%]; lignin: 34.3% [0.8%]) than in *Alchornea* (20.5% [1.0%] and 22.5% [0.2%], respectively).

Litter decomposition rates

Values of k_{total} ranged from 0.0287 to 0.0649 d^{-1} (Table 1). Both species decomposed rapidly, but the rate for *Alchornea* was twice that of *Pterocarpus* and significantly higher for *Alchornea* in Boutroun than for *Pterocarpus* in both streams (Tukey HSD, $P < 0.05$). The fast decomposition of *Alchornea* was evidenced by the absence of leaf litter in CM bags at the last sampling date (Fig. 1). In contrast with leaf species, the differences in k_{total} between streams were weak. Values of $k_{\text{microbial}}$ ranged from 0.0195 to 0.0426 d^{-1} (Table 1). The same between-species discrepancies found for total rates were observed for microbial rates. Microbial decomposition contributed a major portion of total leaf mass loss (Fig. 1) as well as the comparison with invertebrate-driven decomposition (Table 1). Values of $k_{\text{invertebrate}}$ were exceptionally low, ranging from 0.0006 to 0.0045 d^{-1} (Table 1), but were more than twice as high in Boutroun compared to Djodou for both species, a significant difference for *Alchornea* (Tukey HSD, $P < 0.05$). As a consequence, $k_{\text{microbial}}$ largely exceeded $k_{\text{invertebrate}}$ (Tukey HSD, $P < 0.0001$), with discrepancies of 1 or even 2 (Djodou) orders of magnitude.

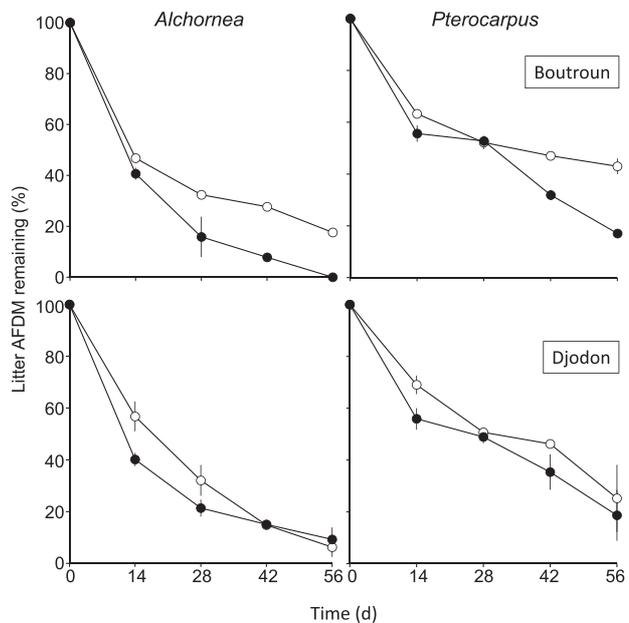


Figure 1. Percentage of remaining ash free dry mass (AFDM) of *Alchornea* and *Pterocarpus* leaf litter in 2 savannah streams, Djodou and Boutroun, in coarse-mesh (●) and fine-mesh (○) bags over time. Mean (SE), $n=3$.

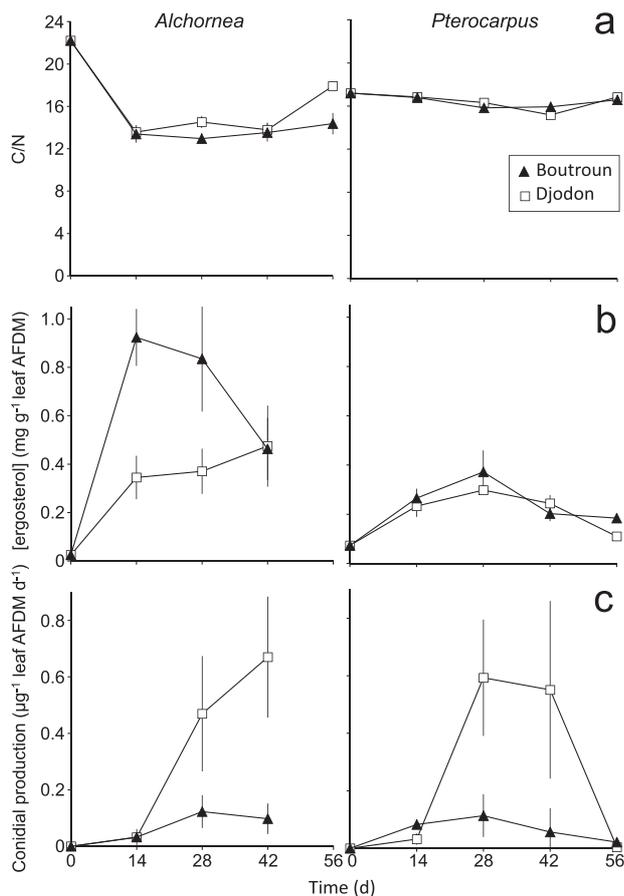


Figure 2. (a) Leaf carbon-to-nitrogen (C/N) ratio, (b) leaf content of ergosterol, and (c) leaf-associated conidial production of *Alchornea* and *Pterocarpus* in 2 savannah streams, Djodon and Boutroun. Because of insufficient leaf mass remaining, data are missing for *Alchornea* leaf content in ergosterol and leaf-associated conidial production at 56 d. Mean (SE), $n = 3$; AFDM = ash-free dry mass.

Changes in C/N ratios

C/N ratios of decomposing leaf litter of *Alchornea* and *Pterocarpus* exhibited different patterns, but these patterns were homogeneous between streams (Fig. 2a). The initial C/N value for *Alchornea* initially dropped to ~13 at 14 d, followed by a regular but moderate increase (up to about 14 and 18 in Boutroun and Djodon, respectively). This decrease and subsequent increase were almost undetectable in *Pterocarpus*, resulting in a relatively stable pattern over the 56 d period.

Leaf-associated decomposers

Fungal dynamics on decomposing litter were assessed through mycelial biomass accrual (ergosterol concentration; Fig. 2b) and reproductive activity (conidial production; Fig. 2c). Ergosterol concentration was minute ($25.0 \mu\text{g g}^{-1}$ leaf AFDM) in senescent *Alchornea* litter prior to submersion, but an initial ergosterol

contamination was detected in *Pterocarpus* ($73.1 \mu\text{g g}^{-1}$ leaf AFDM). *Pterocarpus* in both streams and *Alchornea* in Boutroun showed humped-shape changes in concentration with time, in contrast with the continuous increase found for *Alchornea* in Djodon (Fig. 2c). Ergosterol in *Alchornea* reached a maximum concentration of (mean [SE]) $924 (118) \mu\text{g g}^{-1}$ at 14 d in Boutroun, whereas the peak occurred later in Djodon at $475 (167) \mu\text{g g}^{-1}$ at 42 d. Changes were similar for *Pterocarpus* in both streams, with maxima of $372 (88)$ and $298 (14) \mu\text{g g}^{-1}$ in Boutroun and Djodon, respectively, occurring at 28 d.

The same humped-shape patterns as for ergosterol were found for conidial production (Fig. 2c); however, discrepancies occurred between streams and not between litter species, as was found for ergosterol concentrations. In Boutroun, maxima for both litter species were similarly low at $123 (58)$ and $114 (75) \mu\text{g}^{-1} \text{d}^{-1}$ leaf AFDM for *Alchornea* and *Pterocarpus*, respectively) and occurred at 28 d. In Djodon, conidial production rate reached higher peak values of $670 (214)$ and $593 (202) \mu\text{g}^{-1} \text{d}^{-1}$ at 28 and 42 d for *Alchornea* and *Pterocarpus*, respectively. We identified 17 aquatic hyphomycete species from their conidia released from *Alchornea* litter, 15 of which were also found in *Pterocarpus* (Supplemental Table S1). *Clavariopsis brachycladia*, *Lunulospora cymbiformis*, and *Triscelophorus acuminatus* were the dominant species in both leaf species and streams.

Few leaf-associated macroinvertebrates were collected. They were only found on *Pterocarpus* and all belonged to Baetidae (Ephemeroptera; 6 individuals in total) and Distiscidae (Coleoptera; 3 individuals in total), corresponding to collectors and predators, respectively. No shredders were found on decomposing leaves.

Discussion

In accordance with our first hypothesis, both leaf species decomposed rapidly ($0.0278\text{--}0.0649 \text{d}^{-1}$), consistent with their high nutrient contents and the similarly high decomposition rates ($0.0255\text{--}0.0765 \text{d}^{-1}$) for 2 other litter species reported from a close region of Guinea (Tenkiano and Chauvet 2017). Altogether, these 4 species decomposed at rates slightly below or well above the third quartile (0.0350d^{-1}) of rates calculated for tropical species and sites from a recent global meta-analysis (determined from the appendix S1 in Follstad Shah et al. 2017, subset of 83 observations and 36 tropical tree leaf species). By comparison, the third quartile (0.0259d^{-1}) of rates for temperate species and sites as determined from the same meta-analysis was lower (appendix S1 in Follstad Shah et al. 2017, subset of 569 observations and 90 temperate tree leaf species). Overall,

our findings thus tend to reinforce the principle of faster leaf decomposition in low- compared to high-latitude streams, as revealed by global analyses. The between-leaf species discrepancies in structural compounds and micronutrient contents likely contributed to their 2-fold difference in decomposition rates. Leaf-associated microbial dynamics as reflected by accumulated mycelial biomass was consistent with this difference, but the effect of stream strikingly overwhelmed that of leaf species when examining fungal reproductive activity, a parameter sensitive to stressful environmental conditions (Lecerf and Chauvet 2008).

The absence of shredders in both streams resulted in the supremacy of microbial over invertebrate decomposers, in accordance with our second hypothesis and to an extent documented only from particular tropical streams (Boyero et al. 2015). Overall, the intermittent regime of our savannah streams tended to amplify the detrimental conditions prevailing in the tropics for leaf-decomposer invertebrates. Although speculative and only based on the comparison with different litter species decomposing in nearby permanent streams (Tenkiano and Chauvet 2017), the microbial leaf colonization in these tropical temporary streams seemed to be exacerbated, judging by the uncommonly fast mycelial biomass accrual. Given the strong litter decomposability, the microbial contribution to decomposition tended to overcompensate for the lack of invertebrate decomposers, a phenomenon that would thus even go beyond the simple shift of decomposer type, resulting in decomposition rates maintained across latitudes (Boyero et al. 2011b). Moreover, in contrast with temperate temporary streams (Datry et al. 2011), the processing of leaf litter from riparian trees, which are characterized by high N and P contents, is sufficiently fast to be not affected by flow intermittency.

Leaf quality as a driver of decomposability

A prime driver of decomposition rate of leaves in streams lies in their initial chemical quality (Webster and Benfield 1986, Gessner et al. 2007). High nutrient contents are favourable to the growth, and thus activity, of both microbial and invertebrate decomposers (Bärlocher and Kendrick 1976, Graça 2001). In addition to litter N and P and their stoichiometry, a recent across-biomes and ecosystems experiment stressed the importance of micronutrients like Mg and Ca (García-Palacios et al. 2016). Here, the litter species exhibiting the highest contents in N, P, and Mg (*Pterocarpus*) decomposed slower than the other species (*Alchornea*). By contrast, the much higher Ca content of *Alchornea* was consistent with its faster decomposition. Whether this factor, the lower concentration in lignin (a parameter well

correlated to decomposition rate; Gessner and Chauvet 1994), or both factors were responsible for its higher decomposition rate remains difficult to assert because the set of species examined in our study is limited. Nevertheless, lignin/N ratios of both species (i.e., 9.5 and 11.2 for *Alchornea* and *Pterocarpus*, respectively) as a composite decomposability predictor (Melillo et al. 1982, Enriquez et al. 1993) are relatively close, implying that the 4-fold discrepancy in leaf content in Ca, a critical element for fungal growth and activity (Jenkins and Suberkropp 1995), is likely responsible for the faster microbial (and total) decomposition of *Alchornea*.

P. santalinoides and *A. cordifolia* exhibited markedly high N and P contents in litter, especially for tropical species (although the high N content in *Pterocarpus* remains coherent with its taxonomic status among the N-fixing Fabaceae/Leguminosae). An illustration is their rank as second and eighth highest for N, and second and sixth highest for P, respectively, of 101 tropical leaf species (i.e., including both species plus 99 others listed in supplementary information from Boyero et al. 2017). Clearly, these high nutrient contents may have further contributed to their strong decomposability. Examination of the unchanged C/N ratio in *Pterocarpus* leaves over decomposition (Fig. 1) suggests a “saturation” of their N content, which facilitated decomposition. Similarly, the favourably high Ca and Mg contents found in our leaf species are not consistent with the low values reported for leaf species from the tropics compared to other biomes (García-Palacios et al. 2016). Overall, both tree species thus seemed to contrast with other tropical leaf species, many of which are further characterised by high defence compounds (Stout 1989). While such discrepancies in leaf quality and, in cascade, decomposability among tropical leaves have already been documented (Campbell and Fuchshuber 1995, Boyero et al. 2015), they complicate establishing consistent latitudinal trends.

Predominance of fungal decomposers in savannah streams

Our study highlights the strong involvement of leaf-associated microfungi in litter decomposition in tropical streams, based not only on the relatively high microbial decomposition rates but also on the substantial mycelial biomass accrual and sporulation rates. While supporting some previous findings (e.g., Mathuriau and Chauvet 2002, Abelho et al. 2005), our results contrast with other reports from tropical regions where mycelial biomass and fungal reproductive activity are much lower (i.e., by 1 or 2 orders of magnitude) than in temperate counterparts (Gonçalves et al. 2007, Ferreira et al. 2012, Graça et al. 2016). In our study, peak ergosterol

concentration ($>900 \mu\text{g g}^{-1}$, *Alchornea*, Boutroun, 14 d) was higher than most values reported from the literature (Gessner 1997). Possible explanations lie in (1) the occurrence of fungi other than aquatic hyphomycetes, which would possibly not be involved in decomposition, and/or (2) high mycelial concentration in ergosterol in the dominant aquatic hyphomycete species (i.e., *Clavariopsis brachycladia*, *Lunulospora cymbiformis*, and *Triscelophorus acuminatus*), translating into lower ergosterol-to-mycelium conversion factors (still not documented for these species) and thus mycelial biomass (Gessner and Chauvet 1993). The first explanation is supported by the uncommon early peak of ergosterol, which is generally reported to occur later than sporulation in aquatic hyphomycetes (Gessner et al. 2007). Interestingly, leaf species and stream affected the production of mycelial biomass and fungal reproductive activity differently. In particular, a 6-fold lower peak of conidial production occurred in Boutroun than in Djodou, a finding consistent across leaf species (Fig. 2c). Such depressed fungal activity can be due to the more severe drying regime in Boutroun, which might have altered the pool of aquatic hyphomycete conidia or propagules as inocula for both leaf litter species (Romani et al. 2017).

Exacerbation of the lower implication of tropical invertebrates

The lack of leaf-eating invertebrates in our study represents an extreme case of low involvement of shredders relative to fungal decomposers in the tropics (Boyero et al. 2011a, 2011b). The latitudinal trends hypothesized by Irons et al. (1994) are thus reinforced by our findings, which may be further illustrated by the ratio of microbial decomposition rate to total decomposition rate ranging, for both leaf species and both streams, from 60% (*Alchornea*, Boutroun) to 79% (*Pterocarpus*, Djodou; Table 1). Such values are close to ratios determined for other leaf species and streams of Forested Guinea (range: 60–77%, Fig. 1; cf. Tenkiano and Chauvet 2017). In the present study, the absence of shredders may have resulted from a conjunction of factors, including (1) the detrimental effect of high stream temperature (about 26 °C), amplified by diel oscillations and maxima >30 °C (Boutroun); (2) the hydrological regime altered by prolonged drought periods, limiting the niches for aquatic animals; (3) the possible occurrence of shy detritivores such as crabs and shrimps, which escaped when leaf bags were retrieved; and (4) the potential effect of macroconsumers as predators of insect shredders, as recently shown for shrimps (Andrade et al. 2017). Although we did not collect any of these crustaceans, their presence cannot be precluded because they occur

in nearby savannah streams and could thus explain the (small) discrepancies in leaf mass loss between coarse- and fine-mesh bags, as with shrimps in Forested Guinea (Tenkiano and Chauvet 2017). Our previous hypothesis on the role of shrimps in tropical lowland streams, in contrast with tropical high-altitude streams (Tenkiano and Chauvet 2017), however, is not unequivocally supported by the present findings.

Our streams in Upper Guinea are representative of many savannah streams of West Africa, also characterized by intermittent flow. Such savannah streams are expected to have similarly fast recycling of (micro)nutrient-rich plant organic matter, with microorganisms, particularly fungi, apparently compensating for the potential lack of invertebrate decomposers (i.e., whose stimulated activity maintained high decomposition rates). In some ways, the functioning of these ecosystems resembles that of other savannah streams, like those in Cerrado (Brazil) where microbial decomposers also counter the lack of detritivores (Gonçalves et al. 2007). The apparently tougher leaf litter, however, possibly together with particular environmental settings prevailing in Cerrado, strongly impede decomposition (Gonçalves et al. 2007), thus contrasting with the rapid leaf mass loss observed in Upper Guinea. Future work should better characterize the factors controlling the functioning of savannah streams as well as characterize both their similarities and differences, which excellently illustrate the variability of tropical stream ecosystems (Boyero et al. 2015).

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